UNUSUAL RUSTS ON NYSSA AND URTICASTRUM [1]

E. B. MAINS

(Received for publication February 25, 1921 [2])

During the past year, two very interesting rusts of the family Melampsoraceae have come to the writer's attention. The first of these, upon *Nyssa aquatica*, has remained in the form genus Uredo since its description in 1890 by Ellis and Tracy under the name of *Uredo Nyssae*. While preparing the manuscript of this species for the North American Flora, the writer was fortunate in discovering the telia. A study of this stage shows that the species can not be placed in any established genus and in consequence the following genus is proposed.

Aplopsora[3] gen. nov.

Cycle of development imperfectly known, only uredinia and telia recognized, both subepidermal.

Uredinia pulverulent; urediniospores produced singly, echinulate, the dores obscure.

Telia lenticular, at first covered by the epidermis, soon becoming naked and cinereous from germination; teliospores one-celled, cylindric, in one layer, the wall thin, colorless, smooth, germinating shortly after reaching full size.

Aplopsora Nyssae (Ellis & Tracy) comb. nov.

Uredo Nyssae Ellis & Tracy. Jour. Myc. 6:77. 1890

O + I. Pycnia and aecia unknown.

II. Uredinia hypophyllous, scattered, round, minute, 0.1–0.3 mm. across, early naked, pulverulent, cinnamon-brown, ruptured epidermis inconspicuous; paraphyses peripheral, united below into a short, inconspicuous pseudoperidium, clavate, incurved, 16–26 μ long, the wall 1 μ thick, on convex side above up to 3–4 μ, brownish-yellow; urediniospores obovoid or oblong, 13–17 by 16–26 μ; wall yellow or pale cinnamon-brown, 1 μ, rather closely and finely echinulate, the pores obscure.

III. Telia hypophyllous, gregarious in small groups, round, small, 0.2–0.5 mm. in diameter, at first covered by the epidermis, soon becoming naked, very pale translucent yellow, becoming cinereous from germination; teliospores cylindric, 7–15 by 29–40 μ, rounded above and below, in one layer; wall colorless, very thin, 0.5 μ or less, uniform in thickness, smooth, soon germinating with typical, external basidia.

[1] Contribution from the Botanical Department of the Purdue University Agricultural Experiment Station. Read in part before the Mycological Section of the Botanical Society of America at Chicago, December 29, 1920.

[2] Culture results revised to July 1, 1921.

[3] From ἁπλόος, *simple*, and Ψώρα, *scab*, referring to the telium of one spore layer.

Nyssa aquatica L., Jackson, Miss., Oct. or Nov. 12, 1888, II & III, *S. M. Tracy 1200* (type)[4]; Ocean Springs, Miss., Nov. 4, 1891, II, *F. S. Earle;* Ocean Springs, Miss., Nov. 8, 1891, II, *F. S. Earle;* Great Cypress Swamp, Calvert City, Kentucky, II, *W. W. Eggleston;* obtained from a phanerogamic specimen, no. *5374*, in the herbarium of the New York Botanical Garden by H. S. Jackson.

The uredinia of this rust do not differ markedly from those of a number of genera belonging to the Melampsoraceae. The incurved paraphyses bordering the uredinium and united below into a short pseudoperidium are characteristics which are found in some species of Phakopsora (figs. 1, 2). The urediniospores are borne in a very similar manner to that described by Butler[5] for *Cerotelium Fici* (Cast.) Arth. (*Kuehneola Fici* Butler), the

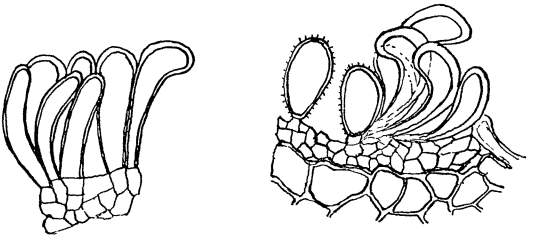

FIG. 1 (Left). Paraphyses of *Aplopsora Nyssae* showing short pseudoperidium at their bases.
FIG. 2 (Right). Portion of uredinium of *Aplopsora Nyssae* showing peripheral position of paraphyses and manner in which urediniospores are borne.

hymenium consisting of a mass of cubical cells upon the uppermost of which the spores are borne (fig. 2). The cells bearing the spores have little to distinguish them from the other cells of the hymenium except that they are separated somewhat from each other. Whether these cells are to be considered as pedicels or whether, as Butler suggests for *C. Fici*, they in turn may develop into spores, cannot be determined from the material at hand, but there is no evidence that the spores form chains.

The telia on the other hand characterize this rust as generically distinct. The teliospores arranged in a one-layered crust of cylindric, one-celled teliospores would place this species in a group with Melampsora, Melampsoridium, and Chnoopsora (fig. 3). From the first two it is distinct tno only in uredinial characters but in that the telium soon ruptures the epidermis and the teliospores germinate at once. In these characters it is much like species of Chnoopsora but differs in the method of teliospore formation. In species of Chnoopsora the teliospores are produced over a period of time due to young sporogenous hyphae developing between the older ones

[4] The description of Ellis gives the host as *N. capitata* and the date as Nov. 1888. Small, in his Flora of the Southeastern United States, gives the range of *N. capitata* as South Carolina to Georgia and Florida. Since other collections of this rust are on *N. aquatica*, it is likely that this collection is also on that host. There is also some confusion as to the date of the collection, some packets being labeled 10/12/1888 and some 11/12/1888.

[5] **Butler, E. J.** Notes on some rusts in India. Ann. Mycol. 12: 76–82. 1914.

and forming teliospores to replace those which have germinated; while in *Aplopsora Nyssae* the teliospores are all formed and matured at practically the same time without subsequent spore production.

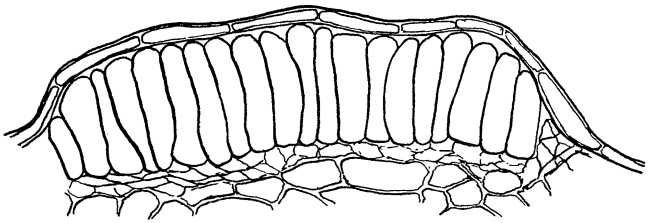

FIG. 3. Section through mature telium of *Aplopsora Nyssae* showing arrangement of spores in one layer.

Just what the complete life cycle of *Aplopsora Nyssae* may be is difficult to say. The early germination of the teliospores without a resting period, if this rust is autoecious, would apparently necessitate the production of pycnia and aecia or pycnia and uredinia immediately following infection or else the development of a systemic mycelium from which such stages would be produced the following spring. The herbarium material available does not show either condition and it is probable that this rust is heteroecious. The aecial stage and probable aecial hosts cannot be foretold definitely. The related genus, Melampsora, has for its aecial stage a Caeoma with either subcuticular or subepidermal pycnia. The alternate hosts belong to a number of genera, mostly, however, conifers. Chnoopsora has for its aecial stage a Caeoma with subcuticular pycnia, the species with known life cycle being autoecious. *Melampsoridium Betulae* (Schum.) Arth. has a peridermium with subcuticular pycnia on Larix. In consequence it would be expected that *Aplopsora Nyssae* would have a Caeoma or a Peridermium for its aecial stage, probably upon some conifer. Specimens of *Caeoma strobilina* Arth. on pine are in the Arthur herbarium from Gulfport and Agricultural College, Mississippi, which may possibly be the alternate stage of the Nyssa rust. Hedgcock and Hunt[6] have reported connecting this rust with a Uredo on Quercus from material collected in Florida. They, however, mention that some of the collections of *Caeoma strobilina* have pseudoperidia and that another rust is represented here, which is unconnected. There is also the possibility that this rust may produce a Peridermium on pine which is at present confused with one of the many species of Peridermium found in the south.

The second rust occurs on *Urticastrum divaricatum* and was received by Dr. J. C. Arthur from Prof. H. W. Anderson who wrote that he had collected it for a Synchytrium but upon examination found what he thought were uredinia. An examination of the material showed that Professor Anderson

[6] **Rhoads, A. S., Hedgcock, G. G., Bethel, E., and Hartley, C.** Host relationships of the North American rusts, other than Gymnosporangiums, which attack conifers. Phytopath. 8: 309–352. 1918.

was correct in considering the fungus a rust and also disclosed that in addition to the uredinia abundant telia were present, most of which were white from the germination of the teliospores. A study of this rust showed that the telium consisted of a crust of one-celled, colorless teliospores, borne in chains of two or three. In these and other characters the rust seemed to belong in the genus Cerotelium. The characteristics and relationships of the rust all pointed to a heteroecious life cycle. Since infection would have to occur in the fall, it appeared quite likely that the aecial stage either developed upon biennial parts of the host such as the needles of some conifer or was systemic. Since conifers were not to be found in the vicinity of the Urticastrum rust at Urbana, it appeared more likely that the aecial stage was systemic. Dr. Arthur immediately suggested *Aecidium Dicentrae* Trel. as the likely aecial stage, since not only is this rust systemic but unlike the usual Aecidium of the region it possesses large, subcuticular pycnia, a characteristic of many of the Melampsoraceous rusts. This conclusion was greatly strengthened by discovering in the herbarium a specimen of the Aecidium collected by Professor Anderson in the same woods earlier in the season. The only apparently serious objection to this connection was the manner of growth of *Bicuculla Cucullaria* (L.) Millsp. (*Dicentra Cucullaria* Torr.). This plant develops and flowers early in the spring and then soon dies down, so that by the time teliospores of the Urticastrum rust are germinating, there is nothing of the Bicuculla plant above ground except an occasional corm. This connection would therefore necessitate an unusual type of infection. *Aecidium Dicentrae*, however, resembles so closely what it was felt the aecial stage should be that sowings were made by placing leaves bearing germinating teliospores of the Urticastrum rust on soil containing corms of *Bicuculla Cucullaria*. The pots of corms were placed out of doors during the winter and then brought into the greenhouse early the next spring. No infection appeared. In spite of this, it was still felt that the rusts of Urticastrum and of Bicuculla were connected. Another attempt was made this spring (1921) by sowing aeciospores of the Bicuculla rust sent from Urbana, Illinois, by Professor Anderson. This sowing produced typical uredinia upon *Urticastrum divaricatum*. The lack of results from the sowings of basidiospores upon the Bicuculla corms may have been due to the effect that the high temperature of the greenhouse had upon the development of the plants, since infected corms sent by Professor Anderson in the summer of 1920 when brought into the greenhouse this spring showed the rust in only a few cases and then only pycnia were produced.

Cerotelium Dicentrae (Trel.) Mains and Anderson comb. nov.

Aecidium Dicentrae Trel. Trans. Wis. Acad. Sci. **6**: 136. 1884.

O. Pycnia amphigenous, somewhat scattered, usually near the margin of the leaf, conspicuous, subcuticular, violet becoming dark chestnut or chocolate-brown, applanate or discoidal, 160–200 μ in diameter by 40–60 μ high; ostiolar filaments wanting.

I. Aecia hypophyllous, subepidermal, scattered over the entire leaf, cupulate, 0.1–0.5 mm. in diameter; peridium white, the margin remaining somewhat incurved, erose; peridial cells rhomboidal in side view, 15–20 by 24–35 μ, overlapping considerably, the outer wall 7–9 μ thick, faintly transversely striate, the inner wall 3–5 μ thick, closely and finely verrucose; aeciospores somewhat angularly globoid or ellipsoid, 12–17 by 13–21 μ; wall colorless, thin, 1 μ or less, closely and very finely verrucose.

Bicuculla Cucullaria (L.) Millsp. (*Dicentra cucullaria* Torr.), Pine Hills, Union Co., Ill., April 24, 1882, *A. B. Seymour 4252;* Madison, Wis., June, 1884, *L. H. Pammel;* Decorah, Ia., May, 1886, *E. W. D. Holway* (Barth. N. Am. Ured. *203*); May 18, 1887 (Sydow, Ured. *497*); Iowa City, Ia., May 7, 1887, *Thos. H. Macbride;* Morning Sun, Iowa, April 16, 1895, *Geo. W. Carver;* Manhattan, Kan., May, 1888 (Kellerm. & Swingle, Kan. Fungi *2*); Topeka, Kan., May 9, 1904, *H. W. Baker* (Ellis & Ev. Fungi Columb. *1903*); Oakwood, S. Dakota, May 9, 1891, *E. N. Wilcox;* Crawfordsville, Ind., June, 1893, *E. W. Olive;* Concordia, Mo., June 20, 1888, May, *C. H. Demetrio* (Rab.-Paz. Fungi Eur. *4335;* Nebraska, 1899, *A. A. Hunter;* Nebraska City, Nebr., April, 1899, *Thornber;* Lancaster, Pa., May 5, 1900, *A. A. Heller 4972;* New York City, Apr. 21, 1913, May 4, 1914, *F. D. Fromme;* Van Cortlandt Park, New York City, April 25, 1912, *F. D. Fromme;* April 20, 1915, *P. Wilson 52;* Williamsbridge, New York City, April 28, 1916, *P. Wilson 230;* vicinity of Grassy Sprain Reservoir, Westchester Co., N. Y., May 27, 1916, *P. Wilson 248;* West Orange, N. J., May 9, 1915, *P. Wilson 59;* Brownfield Woods, Urbana, Ill., May 18, 1919, *H. W. Anderson.*

TYPE LOCALITY: Madison, Wisconsin, on *Dicentra Cucullaria.*

II. Uredinia hypophyllous, few, scattered or in small groups, 1–2 mm. across, round, small, 0.1–0.2 mm., remaining partially covered by the epidermis, pulverulent, yellow, ruptured epidermis evident; paraphyses peripheral, hyphoid, 7–10 by 26–48 μ, thin-walled, colorless, incurved, inconspicuous, not projecting above the ruptured epidermis, arising from a more or less developed pseudoparenchymatous mass of mycelium; urediniospores ellipsoid or obovoid, 18–21 by 20–26 μ, without definite pedicels, attached to short, thin-walled, colorless cells; wall colorless, 1–1.5 μ thick, closely echinulate, the pores obscure.

III. Telia somewhat gregarious in groups 1–3 mm. across, at first arising within and surrounding the uredinia, angular, 0.2–0.5 mm. across, at first covered by the epidermis, becoming naked just before germination, waxy, slightly tinted, becoming flocculose and white from germination, teliospores cylindric or ellipsoid, 10–21 by 29–42 μ, catenulate, in chains of 2 or 3 at the center of the sorus, usually only one at the margin; wall colorless, very thin, uniformly 0.5 μ thick; basidiospores globoid, 10–13 μ in diameter.

Urticastrum divaricatum (L.) Kuntze (*Urtica divaricata* L., *Laportea canadensis* Gaud.), Brownfield's Woods, Urbana, Ill., Aug. 19, 1919, II & III, *H. W. Anderson;* Hannibal, Wis., July 27, 1920, III, *J. J. Davis.*

In the Urticastrum rust we have a telium differing from that of the

Nyssa rust principally in the catenulate method of spore formation, the teliospores developing in chains of two or three (figs. 4, 5). The terminal

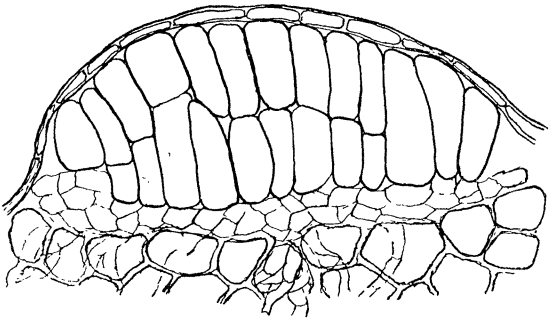

FIG. 4. Section through young telium of *Cerotelium Dicentrae* showing catenulate character of the teliospores.

spore of these chains often germinates before the lower spores are fully developed, and it may be that more spores are produced from the sporogenous cell than show at any one time. The catenulate character of the teliospores indicates that this species is related to a group consisting of such genera as Phakopsora (Physopella, Bubakia, Schroeteriaster), Uredopeltis, Melampsoropsis, Chrysomyxa, Baeodromus, Alveolaria, and Cerotelium. In Alveolaria the arrangement of the teliospores in definite layers which separate from each other, and in Baeodromus the colored thick-walled teliospores with delayed germination, taken with the short life

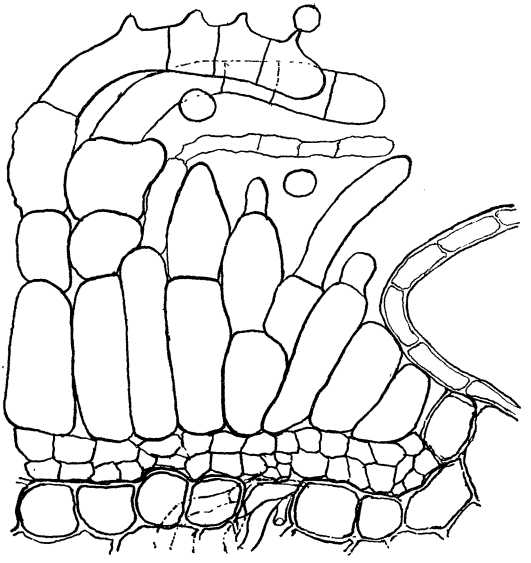

FIG. 5. Section through mature telium of *Cerotelium Dicentrae* showing germination of the teliospores.

cycle of both genera, afford reasons for excluding the Urticastrum rust from these genera. This rust is to be distinguished from species of Uredopeltis and Phakopsora by the colorless walls of the teliospores and by their germination without a resting period. Melampsoropsis, Chrysomyxa, and Cerotelium are genera in which the teliospores germinate without a resting period and are arranged in closely compacted chains. There is no characteristic of the telium which would necessarily prevent this rust from belonging to any of the last mentioned genera, except perhaps that there are a smaller number of teliospores in a chain in the Urticastrum rust than are usually found in the rusts of these genera.

The uredinium of the Urticastrum rust, however (fig. 6), is bordered by a few colorless, incurved paraphyses, and the walls of the echinulate urediniospores are colorless and the spores are borne in a manner similar to that in *Aplopsora Nyssae*. It therefore differs in these respects from species of Melampsoropsis (Chrysomyxa of some authors) which have catenulate, verrucose urediniospores, usually with a surrounding peridium. Chrysomyxa as used by Arthur lacks uredinia and in consequence will be dis-

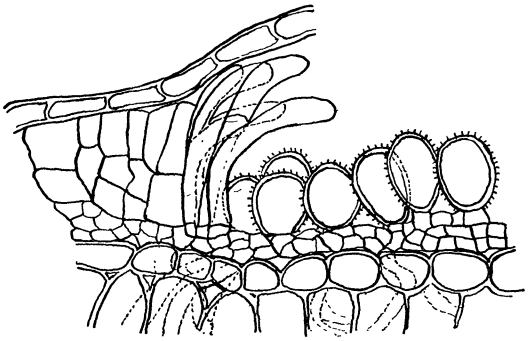

FIG. 6. Section through uredinium of *Cerotelium Dicentrae* showing peripheral paraphyses and manner in which urediniospores are borne.

regarded. This species might be placed in the genus Cerotelium as originally described by Arthur[7] (p. 30), except for the presence of paraphyses in the uredinium instead of a peridium. As a result of the study of additional material Arthur[8] (pp. 505–507) brought together in each of the genera Phakopsora, Cerotelium, and Cronartium species with a peridium, species with paraphyses united below into a pseudoperidium, species with hyphoid or incurved paraphyses, and species with neither peridium nor paraphyses. In the first two genera, species can be found showing gradations, such as incurved colorless paraphyses, colored thick-walled paraphyses, paraphyses united to a greater or less extent to form a pseudoperidium, paraphyses accompanying a peridium, and a peridium only. In consequence the

[7] **Arthur, J. C.** New species of Uredineae. Bull. Torrey Bot. Club **33**: 27–34. 1906.

[8] **Arthur, J. C.** Relationship of the genus Kuehneola. Bull. Torrey Bot. Club **44**: 501–511. 1917.

presence of paraphyses seems no reason for excluding this rust from the genus Cerotelium, the smaller number of teliospores in chains being hardly more than is to be expected in a simpler species of the genus.

The Sydows[9] (pp. 524, 525) consider Cerotelium as a synonym of Dietelia and transfer the type species *Cerotelium Canavaliae* Arth. of the former genus to the latter genus. According, however, to their description of the genus Dietelia, the presence of a peridium around the telium is the most important characteristic of this genus. The telia of *C. Canavaliae* as such do not have a peridium, but when they arise in the old uredinial sorus, as they often do, they are of course surrounded by the peridium there present. Neither does the telial peridium of Dietelia resemble in structure the uredinial peridium of Cerotelium, and for these reasons the writer is of the opinion that Dietelia and Cerotelium should be considered as distinct genera.

In the discovery of the Aecidium of *Cerotelium Dicentrae* the first clue to an aecial stage of rusts of this type has been obtained. The combination of subcuticular pycnia with the cupulate aecium surrounded by a peridium is such as was to be expected from the relationship of the genus Cerotelium to other genera of the Melampsoraceae. The systemic nature of the mycelium is probably specific and accounts for the survival of *Cerotelium Dicentrae* in a temperate climate. The infection of *Bicuculla Cucullaria* by the basidiospores of the rust must occur through the dormant buds of the corm, which are either exposed or immediately below the surface of the soil. Such a type of infection would apparently necessitate a close association of the two alternate hosts and probably accounts for the rather localized occurrence of the rust.

Discussion of Relationships

The character of early maturity and germination of the teliospores has been given considerable prominence in establishing the position of these two rusts. This is a character which in some groups of the rusts is of little or no significance. Here, however, on account of the evident grouping and relationship of rusts with this character it appears to take on considerable importance. Thus if we consider the rusts of the Melampsoraceae which have teliospores germinating without a resting period, they would appear to group themselves in certain definite lines of development. Starting with Aplopsora we have teliospores in a one-layered crust which tardily breaks through the epidermis and germinates at once. In *Cerotelium Dicentrae* we have another step in which a number of the sporogenous hyphae cut off two and three spores in succession to form a compact crust which, on account of its continued spore formation, rather readily ruptures the epidermis. The next type is represented by *Cerotelium Canavaliae* in which the number of spores produced by the sporogenous hyphae is greater and in consequence the epidermis is quickly ruptured and the telium is

[9] **Sydow, P., and Sydow, H.** Monographia Uredinearum 3: 1–726. 1915.

pushed up farther above the epidermis. The telium here is less compact and with less evident lateral coherence of its spore chains. At this point in the development of this group, or a little before, a separation into two distinct lines apparently takes place. In one line there is an increase in the teliospore production from the sporogenous hyphae and a stronger lateral coherence of the spore chains; and hair-like columns of teliospores are formed, giving us the genus Cronartium. In the other line, there is also a greater spore production resulting in longer chains of teliospores, but at the same time the lateral coherence of the chains lessens until finally in the genus Kuehneola there is a complete separation to the base and a falling apart of the spore chains. In consequence of such a development, as might be expected, there is no sharp line of separation between the genera Cerotelium and Kuehneola and some species are in consequence difficult to place, some authors referring them to one genus and some to the other, depending upon their interpretation of the limitations of these genera. As an example of this transition from one genus to the other, we have the following: *Cerotelium Gossypii* (Lagerh.) Arth. possesses a compact telium much like that of *C. Canavaliae*. In *Cerotelium Fici* (Cast.) Arth. and in *C. Vitis* (Butl.) Arth., the teliospore columns are much more loosely arranged, as has been shown by Butler,[10] but the spore chains still hold together and show only a slight tendency to fall apart. In the case of *Kuehneola aliena* Syd. & Butl. and especially in *K. Butleri* Syd. we have two rusts which have been placed in the genus Cerotelium by Arthur (*l. c.* footnote 8, p. 510). In these species, although the spore chains are short and in consequence do not separate as widely as in some species of Kuehneola, the separation is, however, definite; and it would appear best to consider both as species of Kuehneola. Although Dietel[11] (pp. 205–213) was the first to point out the catenulate manner of teliospore formation in Kuehneola as distinguishing it from the genus Phragmidium, yet he retained the genus in the Pucciniaceae, considering it as having developed from Uromyces species on Rubus. Kuehneola was, however, removed to the family Melampsoraceae by Arthur (*l. c.* footnote 7), largely on account of this catenulate character of the teliospore, and these transitional forms support such a disposition of the genus.

The other genera of the Melampsoraceae with teliospores germinating without a resting period are Chnoopsora and Melampsoropsis. The former may be considered as arising from the same source as Aplopsora but diverging upon what may possibly be another line of teliospore formation. The latter may have arisen from a similar source, most likely from a form resembling Melampsora but differing in the development of catenulate urediniospores. The method of urediniospore formation in the Aplopsora-

[10] **Butler, E. J.** The rusts of wild vines in India. Ann. Mycol. **10**: 153–158. 1912. Especially pp. 156–158. Also, *l. c.* footnote 5, pp. 76–79.

[11] **Dietel, P.** Über die Verwandtschaftsbeziehungen der Rostpilzgattungen Kuehneola und Phragmidium. Ann. Mycol. **10**: 205–213. 1912.

Kuehneola line may possibly be considered as representing an original potentiality in the ancestral type which developed in Melampsoropsis but which in the Aplopsora-Kuehneola line became gradually weaker. Phakopsora with the delayed germination of its teliospores may be considered as a similar but less fully developed line from a source similar to that giving rise to Cerotelium.

Both the rusts described above have offered considerable difficulty in the determination of their generic position. It is in this, however, that their principal interest lies, for such species are to be expected as the result of evolutionary development and from such our knowledge of relationships must be obtained. With our present imperfect knowledge of the rusts of the family Melampsoraceae, it is perhaps impossible to gain more than a suggestion of the possibilities which exist. It is felt, however, that these two rusts, *Aplopsora Nyssae* and *Cerotelium Dicentrae*, in their evident relationships point to lines of development, the importance of which will have to be left for future information and studies fully to bring out.

To Prof. H. W. Anderson credit is due for the discovery of *Cerotelium Urticastri* and for the trouble he has taken in solving the life history of this rust. The writer wishes to express his appreciation to Dr. J. C. Arthur for the opportunity of studying the Urticastrum material and for advice and criticism in the study of these two interesting rusts. To Prof. H. S. Jackson acknowledgment is due for aid in obtaining additional material of *Aplopsora Nyssae* in the New York Botanical Garden herbaria and for helpful criticism of this work.

PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION,
LAFAYETTE, INDIANA